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"CONTROLLING SEX IN BUTTERFLIES."

BY CHAS. V. RILEY, M.A.

THE article with the above title by Mrs. Mary Treat, in the March number of the NATURALIST, has attracted a good deal of attention, and most naturalists will be proud that a lady has set the example of making such investigations. But while I fully concur with the authoress in the deduction that the female in insects and especially in Lepidoptera, "requires more nourishment than the male," I cannot follow her in the other conclusion "that sex is not determined in the egg of insects." Were this conclusion well founded it would upset what most physiologists of note believe to be a fundamental principle, viz., that, in the individual, sex is determined at the moment of conception, no matter at what stage of growth it becomes ascertainable by us. That such is the case with the higher animals will scarcely be doubted, and to reason from analogy that it is the case with the whole animal kingdom is quite as natural, though equally as unsafe, as it was in years gone by to argue that *lucina sine concubitu* was an impossibility; or that larval reproduction, in insects, could not possibly take place. It is, therefore, worth while to weigh the evidence for and against the possibility of controlling sex in larvæ.

Mrs. Treat, whom I know to be a good observer, and whom I esteem as a correspondent, had already, in 1871, communicated to me her belief that she could control the sex in butterfly larvæ,

and though I then gave her my opinion that her experiments were by no means satisfactory and conclusive, for the reason that many of the larvæ experimented on died, we find her discoursing in the following unqualified manner in "Hearth and Home" for January 13, 1872, in treating of *Papilio asterias*:—

"When the worms become of the right size cut off their supply of food, and every one will produce a male butterfly! On the other hand even after they have left their food-plant and selected their place to change to the chrysalis, disturb them, make them leave their place, and coax them with a fresh supply of their favorite food, and continue to feed them for about two weeks longer, and all will be females!"

Led by Mrs. Treat's observations to test the question, I last summer conducted a few experiments which resulted very differently from those recorded in the article referred to, and which, after briefly reviewing the article, I will detail. In waiting for some of these results I have been obliged to defer writing this article till the present time.

In the first experiment with *Papilio asterias*, mentioned by Mrs. Treat, some of the larvæ died, and we are not told whether the number experimented with was large or small.

In the experiment with the same insect in 1872 we are told that of seventy-nine specimens that had been labeled males (a few chrysalides having died) three females only were produced. On the other hand those that were well "fed up" and labeled females, produced sixty-eight females and four males. The original number so labeled is not given and it is not stated whether any chrysalides failed to produce the imagines; so that we are left to infer that seventy-two were experimented with and that they all produced the butterfly — a success in rearing which is remarkable.

In the third experiment with twenty larvæ, nine females and eight males were produced, the other three failing.

In the experiment with *Vanessa antiopa* more than half the larvæ died, and in the trials with *Anisota rubicunda* some also died and were parasitized.

Now *Papilio** deposits its eggs singly, and from experience in breeding *asterias*, *Troilus*, *Turnus* and *Ajax*, from the egg, I am satisfied that it would be very difficult to get any great number to hatch on the same day or to become chrysalides or

* I use the term in the old, and not in Mr. Scudder's, sense.

imagines on the same day. The eggs must have been gathered singly, or the larvæ of different ages taken on the same day, or of the same age on different days. Of a given number thus gathered I should expect the sexes to be about equally divided, and we in reality find that of the one hundred and seventy-one larvæ, particularly mentioned, the sexes are almost equally proportioned in number, eighty-eight males and eighty females having been obtained and a few chrysalides (which, as we shall presently see, would most likely be females) perishing.

In *Anisota*, on the contrary, the eggs are deposited in batches and it is more easy to get a number of larvæ of the same age. Mrs. Treat's experience with her thirty-three larvæ is quite opposed to mine with the same species.

Mrs. Treat does not tell us whether she did or did not use any discretion as to the size in selecting her intended males and females, and this is a very serious omission, as by the criterion of size alone among larvæ of the same age, the sexes in many species may be separated with considerable certainty. I regret also that she has not specified at what age, and whether always at the same age, the treatment of "feeding up" and "shutting off" was begun, though we may infer, from what is said, that it was after the last larval molt.

Mrs. Treat speaks of keeping larvæ eating beyond the period of pupating, or rather of preparation for that change, and of "starving" them, as though there was hardly any limit to these processes. Analyzed, what meaning do these expressions convey? Very little. They are deceptive! Most Lepidopterous larvæ, in a state of nature would come under the head of "feeding up" as they usually have an ample supply of food at command, and eat their fill. While, therefore, it is perfectly possible to stunt such larvæ by furnishing them with a scant supply of food, and thus to prolong the period and diminish the amount of their development, it is utterly impossible, in the great majority of cases, to get them to eat after they once commence to prepare for the chrysalis state. This is my firm conviction after ten years of pretty extensive insect-rearing, and I think that most experienced insect-raisers will agree with me. If disturbed after preparing to pupate, most larvæ will repeatedly renew similar preparations, but if too often frustrated they will either transform without the proper preparation or die. They are, doubtless, prompted to forsake their food and

prepare for the transformation by the changes already taking place in the system, and in the great majority of cases the mandibulate is already giving way to the haustellate mouth, and has become impotent to perform its wonted labor. Larvæ can neither be forced nor stuffed beyond a certain limit, and this limit is attained by every well fed larva in a state of nature and in the vivarium, so that if Mrs. Treat's theory had any real foundation almost all insects that were not "starved" ought to be females. A high temperature will cause rapid development, but it does not cause a greater aggregate amount of feeding.

But to my own experiments: Of the six insects chosen, the sexes in some differ in the most remarkable manner, while all show sufficient disparity to render mistakes in separating the sexes impossible. They are, also, all common in this section, so that others will have no difficulty in verifying my facts. Except in the case of *Thyridopteryx* I made no attempt to "feed up;" my efforts all being in the direction of "starving," or, as Mrs. Treat would put it, of producing males. Neither have I relied entirely on my own observation; for, being necessarily absent from home, at intervals, the experiments, with explicit directions, were at such times left in charge of Mr. Otto Lugger and Miss Mary E. Murtfeldt, both well practised in rearing Lepidoptera. I would also premise that the stunting process began from the time of hatching, and that it was carried so far that, of the less hardy species, many died under the treatment. It was, also, especially enforced towards larval maturity. The species chosen were, 1. *Thyridopteryx ephemeræformis* (Haw.); 2. *Orgyia leucostigma* (Sm. and Abb.); 3. *Clisiocampa Americana* (Harr.); 4. *Hyperchiria Io* (Fabr.); 5. *Hemileuca Maia* (Drury); 6. *Anisota rubicunda* (Fabr.).

1. *Thyridopteryx ephemeræformis.*—Two lots: lot 1 consisting at first of between thirty and forty individuals, and abundantly and constantly nourished; lot 2, of thirty individuals and very poorly nourished or "starved." From lot 1, twenty-eight cocoons were obtained, of which fifteen were males and thirteen females, all of them attaining the imago state. From lot 2, eighteen cocoons were obtained, which produced twelve males and six females, two of the females failing to perfect and dying in the chrysalis state, in which the sex is readily determined. The stunted lot produced, on an average smaller specimens, and were later in developing, the first male appearing September 15th

against September 10th, on which day the first male in lot 1 appeared. Some of them, however, were of the usual size.

Besides these two lots which were in small vessels and very strictly watched, I had a great number in a large breeding cage, which were so thoroughly neglected that fully one-half died. No accurate account was kept of them but of upwards of fifty chrysalides obtained, fifteen were females. This is a tough insect and will stand very rough treatment, and the last-mentioned were repeatedly allowed to wander around the cage for three days or more without a particle of food.

2. *Orgyia leucostigma.*— Started with a lot of forty, which were very carefully watched and very insufficiently fed. From them eighteen cocoons were obtained, ten of which were actually females and eight males. I naturally looked for a different result in this case as there is a very perceptible difference in the size of the sexes, and the female larva grows one-third larger than the male requiring, in consequence, a greater amount of nourishment. I had also noticed in previous rearing of this species that the males often passed through but three larval molts, while the females passed through four; but to show that the number may vary in the same species, according to circumstances, Miss Murtfeldt assures me that under this stinting process the former went through four molts like the females. Similarly, Prof. Westwood has informed me that a larva of *Megatoma* [*Tiresias*] *serra* which he once kept on flies and insufficiently fed, lived for three years and molted no less than fourteen times.

3. *Clisiocampa Americana.*— Started with a batch of upwards of fifty just hatched. Obtained only nineteen cocoons from them, the rest dying from hard treatment. Five small females and nine males were obtained, the others dying in chrysalis.

4. *Hyperchiria Io.*— Twelve taken from Baptisia soon after the fifth or last molt. Furnished very stintingly with food. All pupated. Two male moths issued in the fall; four males and three females this spring, three being yet in the chrysalis state. At the same time I had two other lots feeding, with ordinary care, on Sassafras and Amorpha, and in both lots the males have so far preponderated.

5. *Hemileuca Maia.*— One brood of upwards of one hundred from an egg-belt fastened around a peach twig. Endeavored to feed them on peach leaves, which were not to their taste, until

more than half had died. Stinted the rest as much as possible until only thirty-two entered the ground. Of these fifteen produced males and eight females, the rest being yet chrysalides.

6. *Anisota rubicunda.*—About fifty larvæ of all ages, of the first brood, and badly stinted, gave twenty-two chrysalides; and these gave eleven females, seven males—the rest dying. Upwards of a hundred, hatched from eggs deposited in confinement by one of the above females and likewise stinted, gave fifty-six chrysalides.

I watched these with a good deal of interest, as, from the necessarily weakened condition of the parents, I expected a large proportion of males; but I was doomed to disappointment, as but three moths — two females, one male — issued on the 21st and 22nd of May. In examining the remaining chrysalides I find them all dead, and I cannot help thinking that this excessive mortality is attributable to the stinting process they endured as larvæ, more than to any other cause, as the earth containing them was kept in the best condition.

While these experiments were being carried on I had many hundreds of the common silkworm (*Bombyx mori*) feeding on Osage Orange (*Maclura aurantiaca*) a great number of which succeeded admirably out-doors under netting, and others in-doors. Two of the lots in-doors were fed sparingly and not well cared for. No precise records were kept, and very many died; but of the imagines obtained I recollect very well there was no disproportionate number of males.

On the whole, if these experiments indicate anything, they indicate that where more males than females are obtained from stinted larvæ, it is attributable to the fact that the females, being largest and requiring most nourishment, succumb most readily under such treatment; rather than that the sexual characteristics are modified and determined by such treatment. Mrs. Treat's facts are, in some respects, remarkable, but, bearing in mind the influence of the condition of the parents on the sex of the offspring, it will not do to draw conclusions too rashly; for every experienced entomologist knows that occasionally, in a particular brood of larvæ, one sex or the other will greatly preponderate, where no especial treatment was followed in the rearing.

While, therefore, I do not think that the facts yet in our possession, warrant the belief that the quality or amount of food has

any influence in determining sex in the individual once out of the egg, I do believe, with Thomas Meehan, Henry Hartshorne and others, that there is a certain relation between organic vigor and sex, and that the latter may be determined in the offspring by the amount of vigor or vitality — creative or organic force — in the parents, and that the female is in some way connected with increased, and the male with lessened, vitality; for strong arguments may be adduced in favor of such a belief.* Certain curious facts in the natural history of some of our gall-making *Cynipidæ* lend singular weight to these views. From these facts, ascertained by Mr. H. F. Bassett of Waterbury, Connecticut, there can be little doubt that many of the species produce two distinct kinds of galls, alternating with each other, the one vernal, the other autumnal. The former produce flies with a due proportion of the sexes, and the latter produce nothing but large females.† In other words, the directly fecundated and more highly vitalized ova produce nothing but large females, while the parthenogenetic offspring is smaller and composed of both males and females.

The curious facts, as now understood, in the economy of the common hive-bee, seem at first to militate against the conclusion that food has no influence on the sex of larvæ, but in reality they do not, though they indicate that the sex may be altered or determined after partial or imperfect conception has already taken place. All eggs not directly impregnated produce drones or males (*not females*, as "*A. S. P.*," by a singular lapse of thought, has stated on p. 177 of the March number of the NATURALIST), while

* See AMERICAN NATURALIST, vi, pp. 692, 747, and Missouri Entomological Reports, iv, p. 65 and v, p. 85.

† To give a single illustration: A large wool gall—the modification and deformation of a bud—is tolerably common on our black oaks. The flies produced from it (*Cynips q. operator*) are bisexual. Mr. Bassett has witnessed the female depositing in acorns of the same trees on which the wool galls occur. The product of these eggs is a pip-like gall (the *C. q. operatola* of my manuscript) which develops between the cupule and the fruit. It is quite irregular in form, but with the apical end tapering more or less to a point and the basal end rounded. It is greenish when young, yellowish when mature, and the larva rests in a cream-colored ovoid cell, easily freed from its pip-like covering. This gall is generally numerous enough to render the acorns abortive, and I have known it since 1869. In August, 1871, while visiting Mr. Bassett, I collected a number from *Quercus ilicifolia*, and brought them home in the hope of rearing the flies from them. This spring, after a lapse of about twenty months, and just as the oak buds were bursting I succeeded in obtaining a number of flies, every one of them females and agreeing with *C. q. operator* except in being larger. Singularly enough this very year Mr. Bassett succeeded for the first time in finding the producer of the woolly gall, *C. q. operator*, ovipositing in buds; and his description leaves no doubt that the flies he thus discovered are identical with my bred specimens.

those which are impregnated at the will of the mother produce females either partly or fully developed, *i.e.*, workers, or queens. The rule with animals is that the ova perish unless vitalized by the direct influence of the male spermatozoa. Nevertheless parthenogenesis in many of the lower forms of animal life, and especially in insects, is an admitted fact; and what does it imply? To my mind it implies that in exceptional cases, the male element is sufficiently potent to vitalize the ova in the second generation, or that it may endure until succeeding generations; that, in short, to use Owen's words, "the spermatic virtue of the ancestral coitus" may influence the descendants. Von Siebold does not accept this explanation, but there are many facts which indicate that it is the true one, and the male element becomes exhausted in time and is needed sooner or later for the continuance of the species.

Parthenogenesis has repeatedly occurred in species which normally cannot multiply without direct sexual intercourse, *e. g.*, in *Bombyx mori*, *Sphinx ligustri*, etc.; while in a great number of others the embryo, in eggs not directly fecundated, develops up to different stages. What in some species is the exception becomes the rule with others, of which the hive-bee is an example. The male element may be said to possess all degrees of potency in its influence on the reproductive function of its immediate issue, as the embryo in ova not directly fecundated attains all degrees of development before death. In cases of parthenogenesis it is potent enough, vital enough—to cause full development of the offspring for one or more generations, though, in the majority of instances, and especially where this mode of reproduction does not occur as a rule, this offspring is most frequently male. Finally, it may be so potent, as in what is termed thelotoky, that females instead of males are produced.

The ova in a virgin queen bee may, therefore, be said to be already partially fecundated—sufficiently so to produce males or drones; but they must be more thoroughly vitalized, by the direct male influence, before the female sex can be stamped upon them. Even here, however, the sex is not changed after the deposition of the eggs, and it is not the influence of food which produces the change.

Though I believe that the evidence is against Mrs. Treat's conclusion, I hope she will continue her experiments, with that thor-

oughness and exactness of which she is capable. Nature's contrivances for the maintenance of life in all its wonderful and varied phases are inexhaustible, and we are ever laying down rules and theoretical laws, only to find them violated and upset, as we more truly interpret her ways. She is as watchful of the myriad invisible atoms that mantle o'er the pond with green, or of the unseen swarms that fill the air "though one transparent vacancy it seems," as she is of the higher forms of life. Plastic, she conforms in every conceivable and inconceivable way to the wants of her immense family. She shows us

> "The ant's republic and the realm of bees;
> How those in common all their stores bestow,
> And anarchy without confusion know;
> And these forever, tho' a monarch reign,
> Their separate cells and properties maintain,"

and calls loudly on us to read aright and solve her yet many untold secrets.

THE FLORA OF THE DISMAL SWAMP.

BY PROF. J. W. CHICKERING, JR.

A few notes of a recent botanical trip to the Dismal Swamp, that romance of our geographies and Moore's ballad, giving its characteristic flora, with the species found in flower, may not be wanting in interest.

Sunrise, on the morning of April 11th, found our party of two, Mr. William H. Seaman of Washington, and myself, just ready to make the landing at Old Point Comfort. A stroll before breakfast, for a mile or two along the sandy point, brought us to small groves of pitch pine (*Pinus rigida*), interspersed with thickets of dwarf live oak (*Quercus virens* var. *maritima*), here reaching its northern limit, while inside the fortress the true live oak attains quite a large size. The prickly pear (*Opuntia vulgaris*), is scattered along the sand, and on one almost inaccessible edge of the rampart displays its reddish fruit. Along the ramparts occur the bright blue spikes of the grape hyacinth (*Muscari botryoides*), with *Lamium amplexicaule*, *Sisymbrium Thaliana* and *vicia*. A walk of a couple of miles to Hampton